OXYGEN CONSUMPTION AND POPULATION METABOLISM OF SOME POPULATIONS OF ENCHYTRAEIDAE FROM NORTH WALES

F. B. O'CONNOR

Department of Zoology, University College, London

Introduction

The Enchytraeidae have long been known to exist in large numbers in the soil: JEGEN (1920, a, b) and MOSZYNSKI (1928, 1930) reported numbers of up to 150,000 per square metre from highly organic soils. In spite of these early works, the ecology of this numerically important group received little attention for some 25 years. However, the development of reliable quantitative methods for extracting the worms from soil (NIELSEN, 1952—'53; O'CONNOR, 1955) opened the way for large scale population studies. NIELSEN (1954, 1955 a, b) in Denmark, O'CONNOR (1957, 1958) in N. Wales and PEACHEY (1959) in the English Peak district have studied seasonal changes in a number of soil types.

Currently attempts are being made to integrate the results of such population studies with laboratory estimates of the metabolic activity of the worms. NIELSEN (1961) has already expressed his data from a number of sites on a sandy permanent pasture in Denmark in terms of oxygen uptake of the population per square metre. The present paper presents the results of a similar analysis for populations living in a coniferous forest soil in N. Wales.

The site used for this study was a closed stand of Douglas fir *(Pseudotsuga taxifolia)* at an altitude of 250 ft. on the Western foothills of the Snowdonian Mountains. The area is remarkable for the uniformity of its climate; temperature variations are small and rainfall is evenly distributed throughout the year.

Three species of enchytraeids were present in the highly organic, acid soils of the study area. *Hemihenlea cambrensis* (gen. et sp. nov. O'CONNOR, in prep.) was the most abundant, *Achaeta eiseni* (VEJDOVSKY) was less numerous and *Cognettia* (*Enchytraeoides*) *cognettii* (ISSEL) was least abundant. All three are small species, less than 10 mm long as adults. During the period

April 1954 to April 1955 changes in population density of the three species were closely related to temperature, with an early summer peak and a winter minimum. Soil moisture contents did not influence the population significantly during the period of study. This is in marked contrast with the situation reported from Denmark by NIELSEN where summer drought led to a pronounced summer minimum in all but the wettest situations. Thus a comparison between these two studies is particularly valuable.

Population Studies

The data on population changes used for the calculation of population metabolism are as follows:

1) Mean monthly population density
2) Age class composition of the population for each month
3) Mean monthly biomass
4) Mean monthly field temperature.

The estimates of population density used are those previously published (O'CONNOR, 1957), but expressed here as thousands per square metre rather than numbers of worms per soil core. The age class composition and mean live weight of individuals were estimated by measuring the lengths of preserved worms from representative sample units for each month's collection (O'CONNOR, 1958). The relationship between length of preserved worms and live weight was determined by weighing and measuring batches of different sized worms for each species (Table 1). From these measurements it was possible to convert the size distribution of individuals in the population to a weight distribution. For the calculation of population metabolism the worms were classified into 3 or 4 size groups as shown in Table 1, where the

TABLE 1. Size groups and equivalent weights

	Hemihenlea			*Cognettia*			*Achaeta*		
Size group	Mean length mm	Mean wt. µg	Resp. µl O_2/g/hr	Mean length mm	Mean wt. µg	Resp. µl O_2/g/hr	Mean length mm	Mean wt. µg	Resp. µl O_2/g/hr
1	1.0	26	765	1.5	57	990	1.0	20	790
2	3.0	64	605	4.5	190	625	3.0	52	695
3	5.0	160	300	7.5	360	340	5.0	114	430
4	7.0	237	135	—	—	—	7.0	177	255

live weight equivalents for each size group are given for each species. The table also shows the rate of oxygen consumption for worms in the different size groups. Knowing the number per square metre for each month and the distribution of individuals between age groups in the sample, the population biomass and average size of individuals is easily calculated. Table 2 shows

TABLE 2. Percentage and numerical age class composition

Month	Size group	*Hemihenlea*		*Cognettia*		*Achaeta*	
		%	$10^3/m^2$	%	$10^3/m^2$	%	$10^3/m^2$
April . . .	1	53.9	29.51	60.4	34.44	33.0	10.16
	2	40.1	21.95	36.0	20.53	51.4	15.95
	3	6.0	3.28	3.6	2.05	14.5	4.46
	4	—	—	—	—	—	—
May . . .	1	39.8	30.27	68.2	26.38	57.6	27.13
	2	33.1	25.18	27.4	10.60	31.5	14.84
	3	24.5	18.61	4.2	1.62	10.5	4.95
	4	2.6	1.98	—	—	—	—
June . . .	1	33.8	25.90	54.2	24.50	56.6	16.83
	2	33.2	25.44	40.4	18.27	30.6	9.10
	3	27.8	21.30	5.4	2.44	12.5	3.72
	4	5.2	3.98	—	—	—	—
July . . .	1	27.7	29.98	64.6	27.97	62.0	31.36
	2	61.7	66.79	34.0	14.72	31.1	15.73
	3	10.6	11.47	1.4	0.61	6.9	3.49
	4	—	—	—	—	—	—
Aug. . . .	1	25.2	10.88	59.2	18.40	41.4	23.05
	2	66.5	28.42	37.2	11.56	48.8	27.17
	3	8.2	3.50	3.6	1.12	9.8	5.46
	4	—	—	—	—	—	—
Sept. . . .	1	10.7	9.57	66.6	18.16	30.5	17.05
	2	66.0	59.00	31.6	8.62	45.0	25.16
	3	21.2	18.95	1.8	0.49	23.4	13.08
	4	2.1	1.88	—	—	—	—
Oct. . . .	1	11.6	6.22	57.9	28.57	24.3	12.38
	2	67.8	36.38	40.4	19.94	61.4	31.15
	3	20.6	11.05	1.7	0.84	13.0	7.15
	4	—	—	—	—	—	—
Nov. . . .	1	8.8	5.32	39.5	7.32	33.0	21.68
	2	61.7	37.33	48.5	8.99	60.9	40.02
	3	27.9	16.88	12.0	2.22	6.2	4.07
	4	1.6	0.98	—	—	—	—

TABLE. 2. (Continued)

Month	Size group	*Hemihenlea* %	*Hemihenlea* $10^3/m^2$	*Cognettia* %	*Cognettia* $10^3/m^2$	*Achaeta* %	*Achaeta* $10^3/m^2$
Dec. . . .	1	5.9	2.92	42.2	3.22	38.5	8.94
	2	59.9	29.64	54.5	4.16	47.6	11.05
	3	30.1	14.89	3.3	0.24	13.3	3.09
	4	4.1	2.03	—	—	—	—
Jan. . . .	1	7.0	6.05	38.1	7.44	15.7	0.51
	2	60.0	51.89	48.4	9.47	56.7	1.86
	3	29.3	25.34	13.5	2.64	27.6	0.91
	4	3.7	3.20	—	—	—	—
Feb. . . .	1	8.5	5.15	49.0	10.46	35.7	2.24
	2	65.6	39.76	45.1	9.63	45.7	2.86
	3	25.0	15.15	5.9	1.27	18.6	1.17
	4	0.9	0.55	—	—	—	—
March . .	1	4.2	1.87	46.5	9.15	31.7	5.72
	2	71.7	32.00	47.3	9.31	55.2	9.95
	3	22.4	10.00	6.2	1.22	13.0	2.34
	4	1.7	0.76	—	—	—	—
April . . .	1	16.4	14.81	43.8	4.93	42.2	6.05
	2	50.6	45.71	45.7	5.14	46.4	6.66
	3	30.7	27.73	10.4	1.17	11.4	1.63
	4	2.2	1.98	—	—	—	—

the percentage and numerical age class composition for each species for each month. Figures 1, 2 and 3 show the seasonal trend in numbers, biomass and average size of individuals for each species. Figure 2 also shows the mean monthly temperature at 2 cm below the soil surface; all three species lived under the same temperature regime.

Respiration Measurements

Measurements of the oxygen consumption of the worms were made in a Cartesian diver respirometer (HOLTER, 1943). Accurate temperature regulation was maintained so that the temperature did not vary more than ±0.01 °C from the experimental temperature. Heat losses from the thermostat bath were maintained at a constant level by encasing the entire bath in a 1″ thick layer of expanded polystyrene and circulating water from the bath through a cooling coil placed in a second thermostat maintained at 15° C. Heat input was regulated by means of a mercury toluene regulator with proportioning head, operating through a Sunvic E A 4 T Electronic Relay.

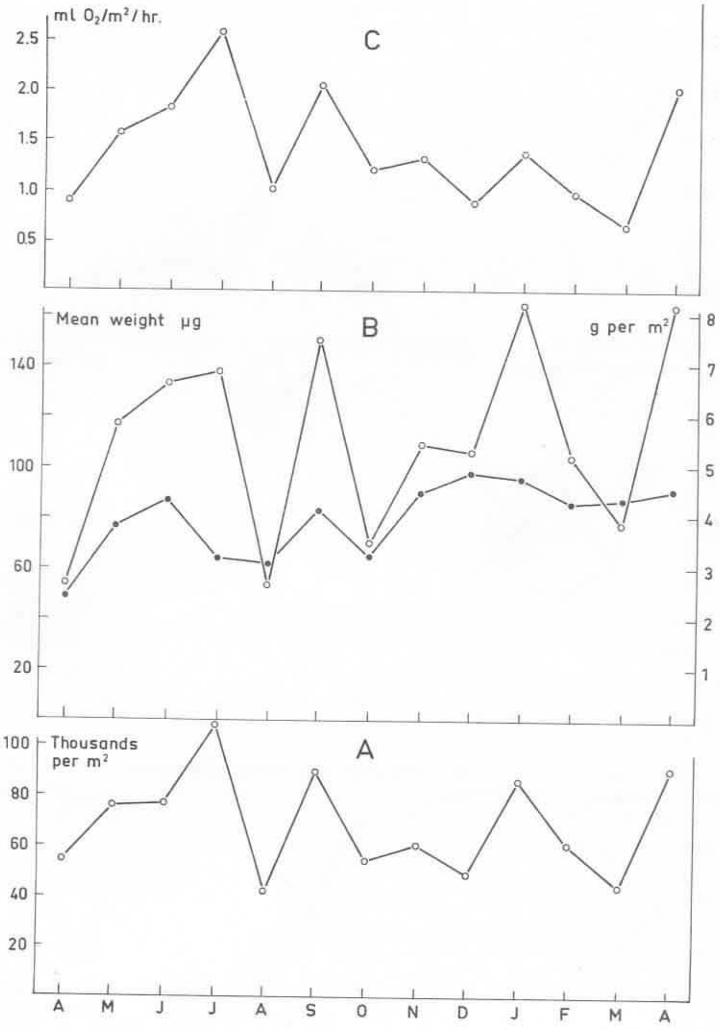

Fig. 1. Monthly means of population density (A), biomass (B ○), weight of individuals (B ●) and rate of oxygen consumption (C) for *Hemihenlea cambrensis*.

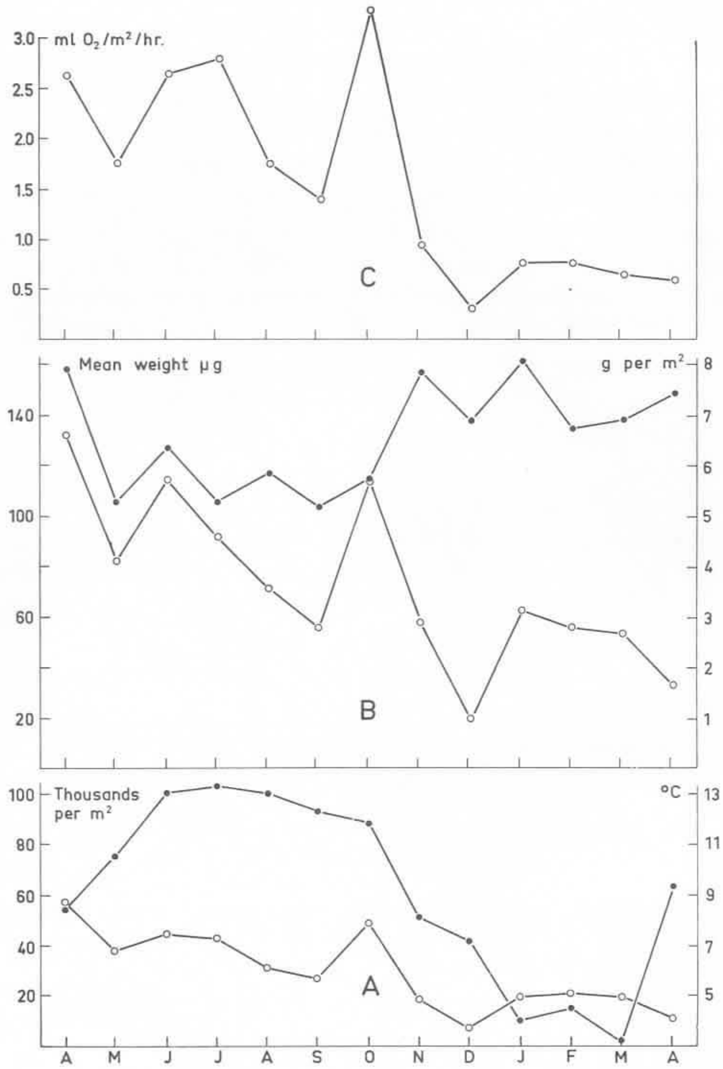

Fig. 2. Monthly means of population density (A ○), temperature (A ●), biomass (B ○), weight of individuals (B ●) and rate of oxygen consumption (C) for *Cognettia cognettii.*

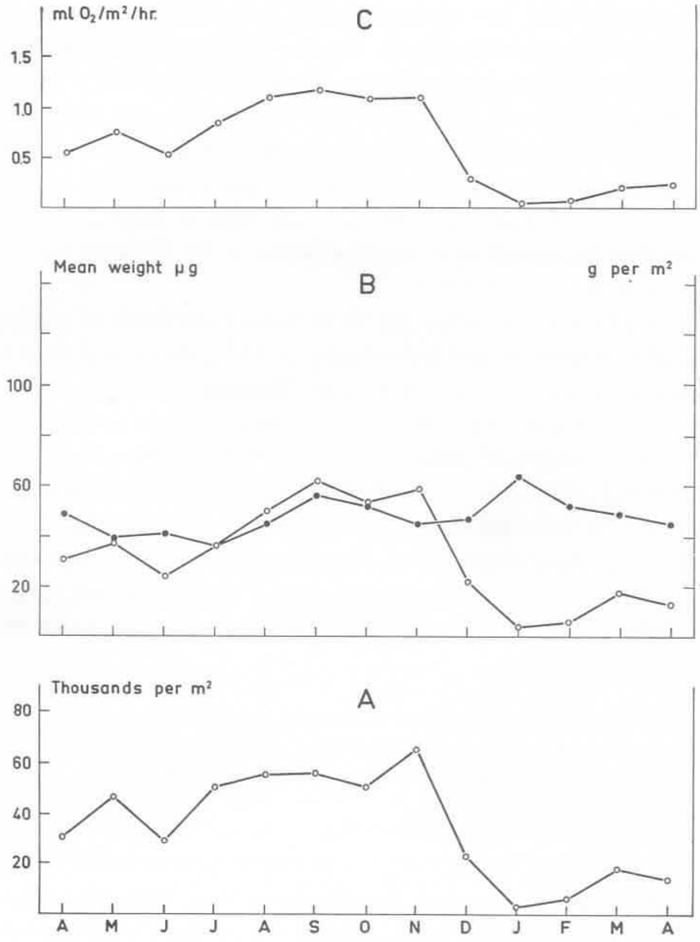

Fig. 3. Monthly means of population density (A), biomass (B ○), weight of individuals (B ●) and rate of oxygen consumption (C) for *Achaeta eiseni*.

Worms for respiratory studies were obtained, either from the original sample site in N. Wales, or from comparable areas in the same region, using the extraction technique developed for the population study (O'CONNOR, 1955). The extraction process relies on the application of heat from above to soil samples placed on a sieve in a water filled funnel, the worms, moving away from high temperatures, pass through the sieve into the funnel whence they can be tapped off. In order to ensure that the worms were in good condition only those obtained during the first half hour of extraction were used. After extraction the worms were stored in water at 10° C for 12 hours before being placed in the respirometer.

Oxygen uptake was measured for 10 or more individuals of each species at 20° C. Worms were placed individually in 75 μl divers and their oxygen uptake measured over a period of 2 hours. Because of the small size of the worms water losses from the surface made it impossible to obtain reproducible values for live weight of single individuals. Instead, their nitrogen content was determined using the micro-Nesslerisation method (THOMPSON and MORRISON, 1951). Respiration was calculated initially as μl O_2/μg N/hr. In order to convert these estimates to oxygen uptake per unit live weight the percentage nitrogen content was determined for 5 weighed batches of 20—50 worms of each species. Table 3 shows the percentage nitrogen content for the three species.

TABLE 3. Mean percentage Nitrogen content

C. cognettii	3.07 ± 0.16
A. eiseni	2.86 ± 0.10
H. cambrensis	2.83 ± 0.09

When the values for oxygen consumption, expressed as μl O_2/g live weight/hr are plotted against μg live weight the curves shown in Fig. 4a are obtained. In all species the rate of oxygen consumption declines steeply with increasing live weight. *Cognettia cognettii* has a higher respiratory rate than *H. cambrensis* and *A. eiseni*, the values for these two species fall on the same curve. *Cognettia cognettii* is very much more active than the other two species both in the divers and in culture slides where their burrowing can be observed (CHRISTENSEN, 1956). The differences in the general level of respiration are supported by observation of the worms.

The respiratory rate also varies with temperature, but the relationship has not been defined for the three species under study. However, measurements

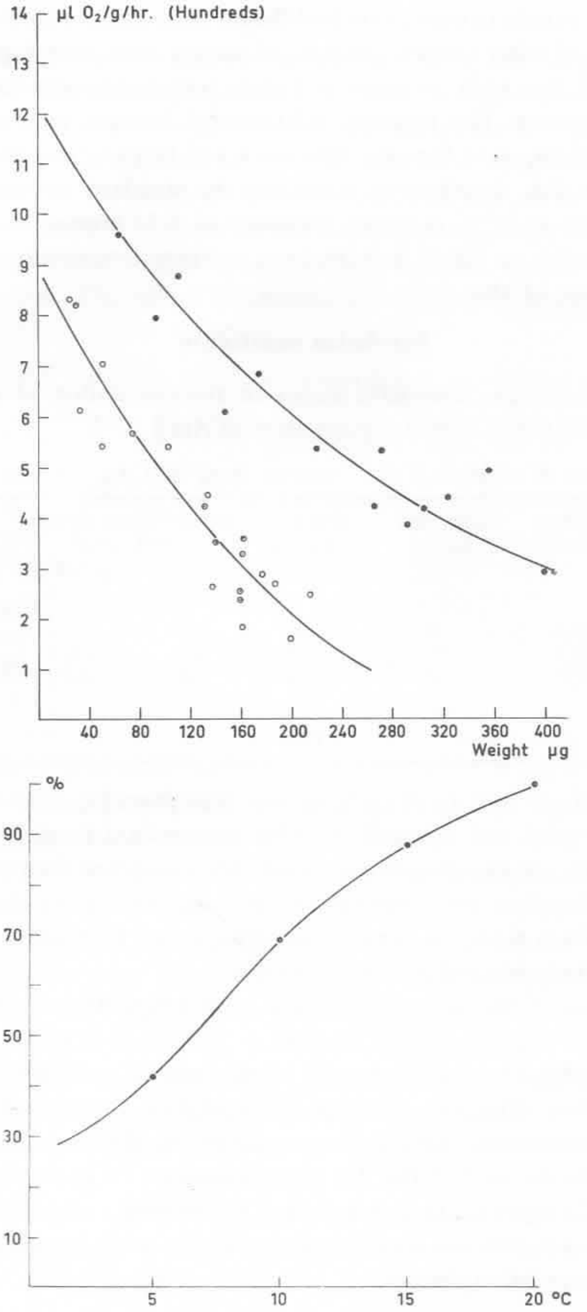

Fig. 4a. The relationship between oxygen consumption and live weight for *Hemihenlea cambrensis* (⊙), *Cognettia cognettii* (●), *and Achaeta eiseni* (○).
Figure 4b. Temperature correction curve.

of the rate of oxygen consumption at different temperatures have been made for a variety of other species. Batches of worms were stored at 5, 10, 15 and 20°C for one week or more and their respiratory rates measured at these temperatures. The resulting relationship between temperature and oxygen upt is shown in Fig. 4b. This work will be described more fully in a later paper. For simplicity in correcting the standard measurements of respiratory rate at 20° C to values for observed field temperatures, the rate at 20° C is taken as 100 % and the rates at lower temperatures expressed as a percentage of this.

Population metabolism

Table 4 shows the successive stages in the calculation of population metabolism for the *C. cognettii* population in April 1954.

TABLE 4. Population metabolism of *C. cognettii*, April 1954, Field Temperature 8.4° C

size group	numbers $10^3/m^2$	mean body wt. µg	biomass g/m^2	oxygen consumption µl $O_2/g/hr$ at 20° C	at 8.4° C	population metabolism ml $O_2/m^2/hr$
1	34.4	57	1.963	990	564.3	1.107
2	20.5	190	3.901	625	356.2	1.389
3	2.0	360	0.739	340	193.8	0.143
Totals			6.603			2.640

The respiratory rate in µl $O_2/g/hr$ was read from Fig 4a for each size group. This value was corrected to field temperature from Fig. 4b. The oxygen uptake per square metre for each size group was then obtained by multiplying together the temperature corrected respiratory rate and the biomass. The values for the separate size groups were then added to give the total population metabolism for the month.

Similar calculations were made for each species population for each month and the results plotted in Figs 1, 2 and 3.

NIELSEN (1961) has discussed some of the general problems involved in using laboratory estimates of oxygen consumption for the calculation of population metabolism; no detailed consideration of this problem is given here. It is however, certain that the experimental errors in the measurement of the rate of oxygen uptake, as indicated by the scatter of points about the size-respiration curves, are small in relation to the errors associated with the estimate of population density.

Discussion

1) **The general level of population metabolism.** In recent years the relative importance of soil dwelling organisms has been measured using the criteria of abundance, biomass and, more recently, metabolic activity (MURPHY, 1953; MACFADYEN, 1962). It is therefore of interest to compare the ranking of three species of enchytraeid worms in a single habitat according to these three criteria. Table 5 summarises the mean annual levels of population density, biomass and metabolic activity for the three species and for the total population. The values for individual species are also expressed as percentages of the population totals.

TABLE 5. Summary of annual levels of populations density, biomass and metabolism

	Mean density		Biomass		Metabolic activity			
	$10^3/m^2$	%	g/m^2	%	ml O_2/m^2/hr.	l O_2/m^2/yr.	%	kcal/m^2/yr.
Hemihenlea	68.7	51.2	5.512	51.0	1.42	12.4	39.2	59.2
Cognettia	30.9	23.0	3.667	34.0	1.57	13.5	43.7	64.5
Achaeta	34.7	25.8	1.615	15.0	0.62	5.4	17.1	25.8
Total population	134.3		10.794		3.61	31.3		149.5

It is apparent that the ranking of the three species differs according to the criterion used. *Hemihenlea* contributes 51 % to both total population density and biomass but only 39 % to population metabolism, *Cognettia*, though least important numerically, ranks second in order of biomass and has the highest population metabolism. *Achaeta* is the least important in terms of biomass and population metabolism but is second in order of abundance. These differences in ranking illustrate the dangers involved in using numbers or biomass alone as a measure of the importance of a population.

Figures for the calorific equivalent of oxygen consumption can only be calculated approximately. The respiratory quotient has not been determined for these, nor for any other Enchytraeidae. However their diet consists of a mixture of organic debris, fungi, bacteria and probably protozoa and so it seems safe to use the calorific equivalent of 4.775 kcal/l O_2 given by HEILBRUNN (1947) for animals feeding on a mixed substrate. The calculated values for the annual calorific equivalent of oxygen consumption are given in Table 5.

It is not at present possible to arrive at a figure for the total calorific requirement of the population. Insufficient data is available on the calorific requirement for body building, either for individual growth or replacement of individuals in the population. Data on the reproduction and mortality rates for the population and on growth rates and longevity of individuals will be required for a final assessment of the relative magnitude of the respiratory and body building requirements. Nonetheless, as MACFADYEN (1962) points out, it is likely that the respiratory requirements will be large in relation to the whole.

2) **Seasonal trends.** In all species there is a tendency for population densities to be higher in the summer than in winter, but in no case are the differences between summer and winter very marked. It has been shown previously (O'CONNOR, 1957, 1958) that the seasonal trend in density is positively correlated with temperature change. The small amplitude of density variation is related to the small range of temperature fluctuation in this remarkably temperate area. The average weight of individuals in the populations is, in all cases, lower in summer than in winter. Thus, while population biomass follows the same course as does density the seasonal differences are less marked. Population metabolism will increase with biomass and with temperature, but is inversely related to the size of individuals in the population. The result of interaction between these factors is to exaggerate the relative magnitude of the differences between summer and winter.

It is apparent that the seasonal trend in population density, biomass, metabolism and the average weight of individuals is similar for all species and that the amplitude of variation in all these parameters is small.

Examination of Figs. 1—3 shows that the ranking of the species populations described in Table 5 is maintained throughout the year in the case of population density and biomass. When the curves for population metabolism are compared, however, it can be seen that the relative contribution of the species populations differs between winter and summer. Throughout the year *Achaeta* contributes least to population metabolism but *Cognettia* is dominant in summer and *Hemihenlea* in winter. This reversal results partly from the greater proportional reduction of the *Cognettia* population in winter, but is also related to the slope of the size-respiration curves (Fig. 4a). It is apparent from these curves that increase in the weight of individuals reduces the respiratory rate relatively more for *Hemihenlea* than for *Cognettia*. Thus the winter increase in body weight and the greater decrease in biomass combine to bring the winter population metabolism of *Cognettia* below that of *Hemihenlea*.

3) **Comparison with populations from other situations.** For the purpose of comparison with other situations the population biomass, metabolism and

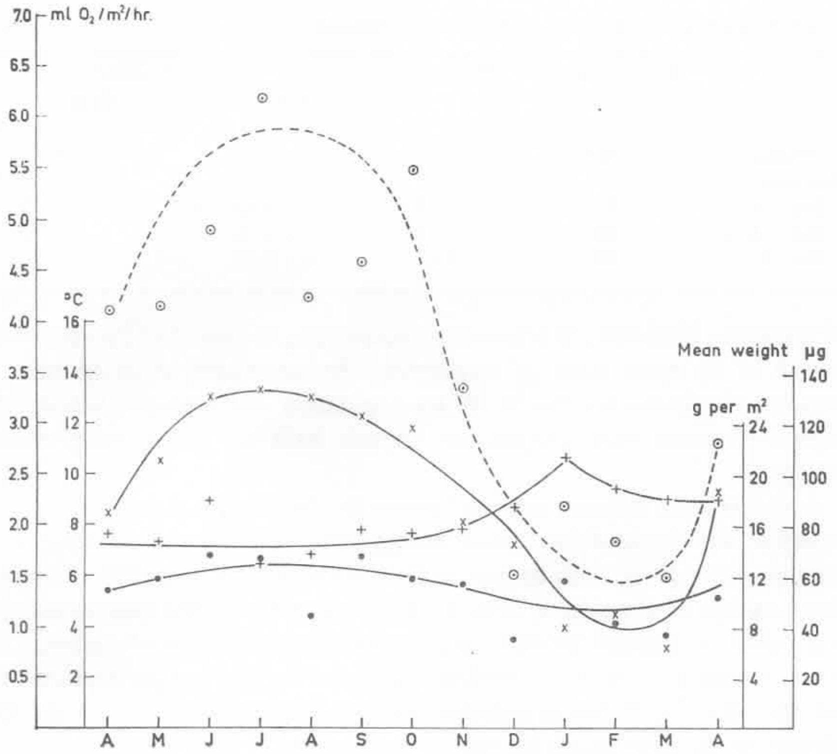

Fig. 5. Seasonal trends in population metabolism (⊙), biomass (●), mean weight of individuals (+) and temperature (×) for the total population.

mean body weight have been plotted for the entire population in Fig. 5. Because of the marked climatic contrast between Denmark and N. Wales it is instructive to compare the results of similar studies in the two countries. Data for the Danish populations are all taken from Nielsen (1961). The comparison already made between seasonal fluctuations in population density (O'Connor, 1957) can now be extended to include a consideration of population metabolism.

Table 6 summarises the mean annual values of population density, biomass and respiration for the total N. Wales population and for Nielsen's Stations 1, 4 and 18; these are a series showing decreasing effects of summer decimation of the population due to drought.

The comparison between general levels of metabolic activity is not worth pursuing in detail because of differences in the species composition between the N. Wales and the Danish populations; the latter consisted predominantly

TABLE 6. Comparison between N. Wales and Denmark

	Density $10^3/m^2$	Biomass g/m^2	Metabolic activity ml $O_2/m^2/hr$	 l $O_2/m^2/yr.$
N. Wales	134.3	10.79	3.61	31.3
Stn. 1	44	2.97	0.84	7
Stn. 4	30	3.03	1.10	10
Stn. 18	74	10.5	3.70	32

of the genus *Fridericia*. It is however encouraging to note that the estimates are all of the same order of magnitude. The remarkably close agreement between the figures for the N. Wales population and Nielsen's Station 18 cannot be more than coincidence, though both are permanently moist situations.

A comparison between seasonal trends in the two countries is more instructive. It is generally accepted that the Enchytraeidae form a relatively homogeneous group with respect to their reaction to environmental conditions and so a comparison between seasonal trends in the two situations will not be invalidated by differences in species composition of the populations. Figure 6 shows the population metabolism and temperature curves for the total N. Wales population and for Nielsen's Stations 1 and 18 plotted on the same graph for ease of comparison.

There is a general similarity in the form of the curves for the N. Wales population and Nielsen's Station 18; both these are permanently moist situations. In both cases the seasonal variation in the average size of individuals in the population is small and this factor has only a small influence on changes in respiratory activity. Population density and biomass are closely related to temperature with summer maxima and winter minima. This fact, combined with the increased respiratory rate at high temperatures produce a summer maximum in population metabolism. Because of the greater range of temperature variation in Denmark the amplitude of variation in population metabolism is greater.

Both these situations can be contrasted with Nielsen's Station 1 where the population was severely depleted by drought during April—June. NIELSEN (1955b) has shown that the population recovered from drought with the onset of rain in the autumn by the mass hatching of cocoons already in the soil since before the drought. This results in an almost complete replacement of the population after drought by a population of small

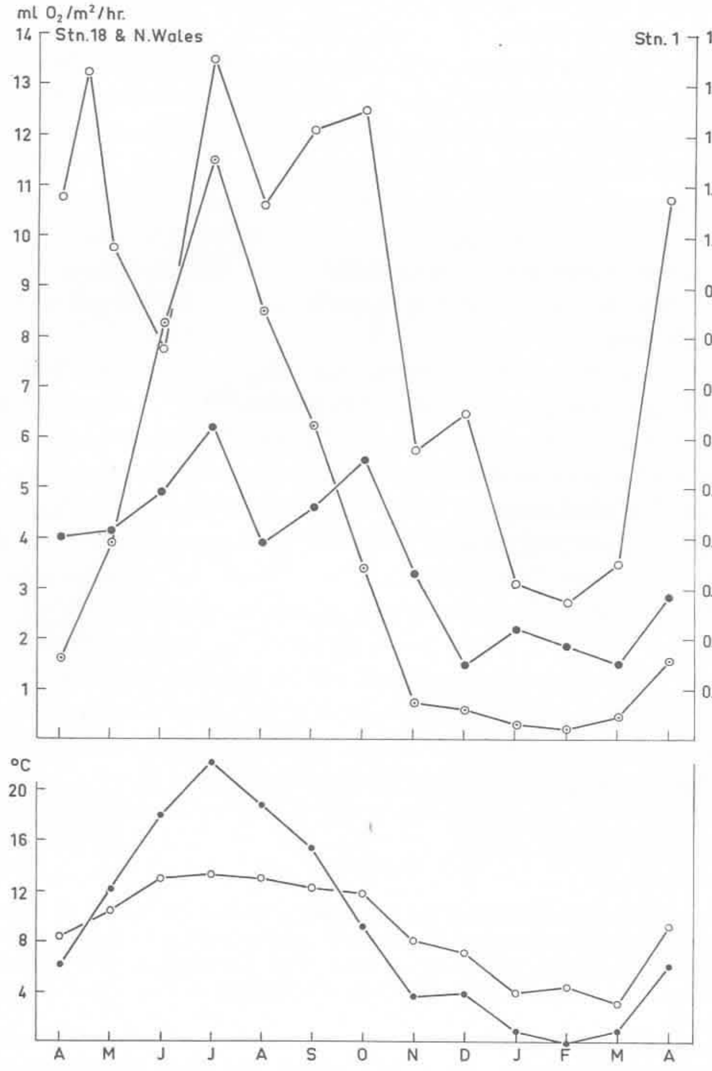

Fig. 6. Comparison of population metabolism in North Wales and Denmark. Population metabolism: — N. Wales (●), Denmark Stn. 1 (○), Stn. 18 (⊙). Note different scale for Stn. 1. Temperature: — N. Wales (○), Denmark (●). Danish figures from NIELSEN (1961).

newly hatched individuals. Thus the average weight of worms drops sharply during the recovery phase.

The effect of these changes on population metabolism is to override the association with temperature found in permanently wet situations. During the onset of drought population metabolism follows the fall in biomass in spite of high temperatures. During recovery from drought the small size of individuals results in an increase in respiratory rate which is sufficient to counteract the decrease in respiratory rate due to falling temperatures in the autumn. From November, on through the winter months, temperature once again becomes the most important factor in determining the rate of population metabolism.

Thus, just as drought can override the effects of temperature in determining the course of density change (O'CONNOR, 1957) it can also override the relationship between temperature and population metabolism.

The present paper presents results which form part of a programme aimed at the complete elucidation of energy utilisation by the soil dwelling Enchytraeidae. In the simplest possible terms this will involve putting quantitative values to the energy flow equation:

Rate of assimilation of calories = rate of loss in respiration
+ rate of use in body building.

In order to complete this equation it will be necessary to determine either the calorific value of the food assimilated or the calorific equivalent of biomass turn over in the population. Either approach presents many difficulties but the first alternative is probably the more fruitful.

Summary

Data from a laboratory study of the respiratory rate of three species of enchytraeid worms are used in the calculation of population metabolism for populations living in a coniferous forest soil in N. Wales. Annual mean rates of respiration ranged from 5 to 13 l O_2/m^2/year. The seasonal trend in population metabolism was related primarily to temperature.

The general level of population metabolism and the seasonal trend are compared with figures for Danish populations recorded by Nielsen. The greater temperature range in Denmark leads to fluctuations of greater amplitude but drought can greatly modify the course of the seasonal trend.

References

CHRISTENSEN, B., 1956. Studies on the Enchytraeidae 6. Technique for culturing Enchytraeidae with notes on cocoon types. Oikos, **7**, 302—307.

HEILBRUNN, L. V., 1947. An outline of general physiology. (2nd. Ed.) Saunders, London.

HOLTER, H., 1943. Technique of the Cartesian diver. C. R. Trav. Lab. Carlsberg, Sér. chim., **24**, 399—478.

JEGEN, C., 1920a. Zur Biologie und Anatomie einiger Enchytraeiden. Vjschr. Naturf. Ges. Zürich, **65**, 100—208.

———, 1920b. Die Bedeutung der Enchytraeiden für die Humusbildung. Landw. Jb. Schweiz, **34**, 55—71.

MOSZYNSKI, A., 1928. Influence des conditions écologiques sur la distribution des Enchytraeides. Kosmos. Journ. Soc. Polon. Nat. Kopernik., **53**, 731—766.

———, 1930. Répartition quantitative des Enchytraeidae dans différents milieux. Ann. Mus. Zool. Polon., **9**, 65—127.

MACFADYEN, A., 1962. Animal ecology, aims and methods. 2nd Edn. Pitman, London.

MURPHY, P. W., 1953. The biology of forest soil with special reference to the mesofauna or meiofauna. J. Soil. Sci., **4**, 155—193.

NIELSEN, C. O., 1952–3. Studies on the Enchytraeidae 1. A technique for extracting Enchytraeidae from soil samples. Oikos, **4**, 187—196.

———, 1954. Id. 3. The microdistribution of Enchytraeidae. Oikos, **5**, 167—178.

———, 1955a. Id. 2. Field studies. Nat. Jutl., **4**, 1—58.

———, 1955b. Id. 5. Factors causing seasonal fluctuations in numbers. Oikos, **6**, 153—159.

———, 1961. Respiratory metabolism of some populations of enchytraeid worms and free living nematodes. Oikos, **12**, 17—35.

O'CONNOR, F. B., 1955. Extraction of enchytraeid worms from a coniferous forest soil. Nature, London, **175**, 815—816.

———, 1957. An ecological study of the enchytraeid worm population of a coniferous forest soil. Oikos, **8**, 161—199.

———, 1958. Age class composition and sexual maturity in the enchytraeid worm population of a coniferous forest soil. Oikos, **9**, 272—281.

———, In. prep. *Hemihenlea cambrensis* (gen. et sp. nov.) a new enchytraeid worm (Oligochaeta) from North Wales.

PEACHEY, J. E., 1959. Studies on the Enchytraeidae of moorland soils. Thesis (Unpub.) Durham University Library.

THOMPSON, J. F. and G. R. MORRISON, 1951. Determination of organic nitrogen. Control of variables in the use of Nessler's reagent. Analyt. Chem., **23**, 1153—1157.